RESEARCH ARTICLE

Species composition and community structure of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) compared among savanna and forest formations in the southwestern Brazilian Cerrado

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ABSTRACT. Although dung beetles are important members of ecological communities and indicators of ecosystem quality, species diversity, and how it varies over space and habitat types, remains poorly understood in the Brazilian Cerrado. We compared dung beetle communities among plant formations in the Serra Azul State Park (SASP) in the state of Mato Grosso, Brazil. Sampling (by baited pitfall and flight-interception traps) was carried out in 2012 in the Park in four habitat types: two different savanna formations (typical and open) and two forest formations (seasonally deciduous and gallery). A total of 5,400 individuals collected comprised 57 species in 22 genera. Typical savanna had the greatest species richness and abundance, followed by open savanna and deciduous forest, while the gallery forest had the fewest species but high abundance. Tunnelers (one of three main nesting behavior guilds) showed the greatest richness and abundance (except in the gallery forest, where one dweller species was extremely abundant) in all plant formations. We found that species richness and abundance of the dung beetle community are influenced by differences among plant formations. Habitat heterogeneity in the different plant formations along with anthropic influences (fire, habitat fragmentation) are cited as important factors that explain guild and species richness and distribution patterns. These results emphasize the importance of protected areas, such as SASP, for the maintenance and conservation of species diversity in the Brazilian Cerrado.

KEY WORDS. Beetle community, guilds, habitat structure, inventory, RAPELD, Serra Azul Park.

INTRODUCTION

Dung beetles, found world-wide, are extremely diverse in the tropics (Halffter and Matthews 1966, Davis and Scholtz 2001, Scholtz et al. 2009). Often used as ecological indicators in diversity studies (Spector and Forsyth 1998, Halffter and Favila 1993), dung beetles are taxonomically well known, easily sampled using low-cost and standardized protocols (Halffter and Favila 1993, Gardner et al. 2008), which permits comparisons of community structure at different times or locations (Hernández et al. 2019). Dung beetles also are important in ecosystem maintenance due to their influences on nutrient cycling, secondary seed dispersal, soil aeration, and parasite suppression (Halffter and Favila 1993, Nichols et al. 2007, 2008, Scholtz et al. 2009).

Dung beetles can be divided into three main nesting behavior guilds (hereafter, simply "guild") by the way they use the food resource: (1) rollers form balls of feces or carrion that they then roll and bury some distance from the source, (2) tunnelers bury

feces or carrion at or very near the source, and (3) dwellers simply use the feces or carrion at the source without either tunneling or burying (Halffter and Matthews 1966, Halffter and Edmonds 1982, Hanski and Cambefort 1991). These resource-use guilds cause the dung beetle community to be sensitive to variation in landscape conditions, including soil texture, humidity and temperature (Halffter et al. 1992, Almeida et al. 2011, Silva et al. 2015) and to habitat perturbation (Halffter et al. 1992, Halffter and Favila 1993, Almeida et al. 2011, Filgueiras et al. 2011).

Assemblages of dung beetles respond quickly to habitat structure (Durães et al. 2005, Almeida and Louzada 2009, Costa et al. 2009). Assemblages reach their greatest diversity in well-preserved environments in which community structure and guilds are distinct (Halffter 1991, Halffter and Arellano 2002). As a consequence, spatial variation in dung beetle community occurs across landscapes formed by mosaics of different environmental condition and habitat type. Thus, different plant formations influence the different dung beetle community structures, such that each plant formation (local diversity) is essential for the maintenance of regional diversity (Halffter and Arellano 2002, Spector and Ayzama 2003, Almeida and Louzada 2009).

Landscape-wide variation in community structure is a consequence of adaptive response by dung beetles to different formations, such as open and dry savanna versus shady and humid forest. For example, differences in food resources and microclimate conditions for exploitation of feces (Durães et al. 2005), structural heterogeneity resulting from plant stratification (Almeida and Louzada 2009, Silva et al. 2010), forest-fragment size and isolation (Milhomem et al. 2003, Silva et al. 2010), and temperature variation (Endres et al. 2007) are all important factors. Thus, species richness in forests and open areas can be favored by differences in trophic specialization, habitat selection, and resource use behavior by the different species and guilds of dung beetles (Hernández et al. 2019).

The Brazilian savanna (locally known as Cerrado) occurs in much of the center of Brazil, where soils, geology, climate, and vegetation (forests, savannas, and grasslands) are all quite variable, resulting in a variety of savanna formations (Silva et al. 2006, Ribeiro and Walter 2008). Recognized as a global hotspot of diversity, the Cerrado is occupied by many species that are important for conservation (Myers et al. 2000), and faces many problems, but mostly habitat loss due to the rapid rate of conversion for agriculture and other anthropic uses. These can cause habitat loss and fragmentation, invasion by exotic species, erosion, and species loss at local and regional scales (Brannstrom et al. 2008, Klink and Machado 2005, Carvalho et al. 2009, Santos et al. 2017). Despite the importance of and threats to savannas, biodiversity is surprisingly poorly studied in the Cerrado, especially for invertebrates (Myers et al. 2000, Klink and Machado 2005). Dung beetles, because of their diversity and species-specific habitat-use specializations, can provide very important information about ecological processes in savannas (Durães et al. 2005, Almeida and Louzada 2009, Silva et al. 2010, Daniel et al. 2014).

Here, we compare dung beetle community structure and composition among four vegetation formations (typical savanna, open savanna, deciduous forest, and gallery forest) in Serra Azul State Park (hereafter, SASP), a protected park in the state of Mato Grosso, Brazil. Specifically, we test how taxonomic and guild composition and structure are associated with vegetation formation in the study area. Based on the geographical location of the SASP and the predominance of savanna formations in its limits, we hypothesize that these habitats show high richness and abundance, and that the composition and guild structure vary according to the particular habitat types in which they are found.

MATERIAL AND METHODS

We studied dung beetles in the SASP, in the state of Mato Grosso (15°51'S; 52°16'W), Brazil (Fig. 1). SASP was created in 1994 encompassing around 110 km² at 350–750 m elevation. The dry season (May to September) and wet season (October to April) are well-defined, with annual rainfall of 1447–1528 mm, and temperature varying from 21.8–28.1°C (Pirani et al. 2009). Following RAPELD (method adopted in long-term ecological research sites – PELD in Portuguese), plots were established in the state park. Collection was carried out in December 2012 on 10 plots, with a distance of 1000 m between plots of 250 m transects that maintain a constant elevation (Magnusson et al. 2005). The vegetation formation in each plot was previously classified following the protocol of the Biodiversity Research Program (with the Brazilian acronym PPBio, Programa de Pesquisa em Biodiversidade) adapted locally by the ComCerrado Network (Fig. 1). Four plots were classified as typical savanna, another four as open savanna (both savannas had 356 to 1463 trees ha⁻¹), and the other two plots were gallery forest (684 trees ha⁻¹) and deciduous forest (586 trees ha⁻¹). Vegetation height in both savannas varied from 1 to 13 m, while in both forests height varied from 2.2 to 25 m (Sousa et al. 2019).

Each 250 m transect was divided into 5 sampling points 50 m apart (the span of 200 m was within the 250 m). At each point, three pitfall traps were established at the angles of a triangle (each leg 3 m in length) centered on the point. Pitfalls were 19 cm diameter, 11 cm deep round plastic containers placed in the ground with the rim at the level of the soil surface. A roof to prevent pitfalls from filling with rainwater was built over each. A smaller recipient was placed at an edge of each pitfall to contain approximately 20 g of human feces used as bait. Beetle captures in the three pitfalls were combined to make each point a replicate, for a total of five sampling points per transect in ten transects. Two flight interception traps (FIT) were placed in each of the two savanna types, and one in each forest type, for a total of six traps. To preserve captured insects, approximately 250 ml of saline-detergent solution was placed in each pitfall and flight interception trap. After traps were open for 48 hours, trap contents were placed in 70% alcohol and transported to the laboratory at
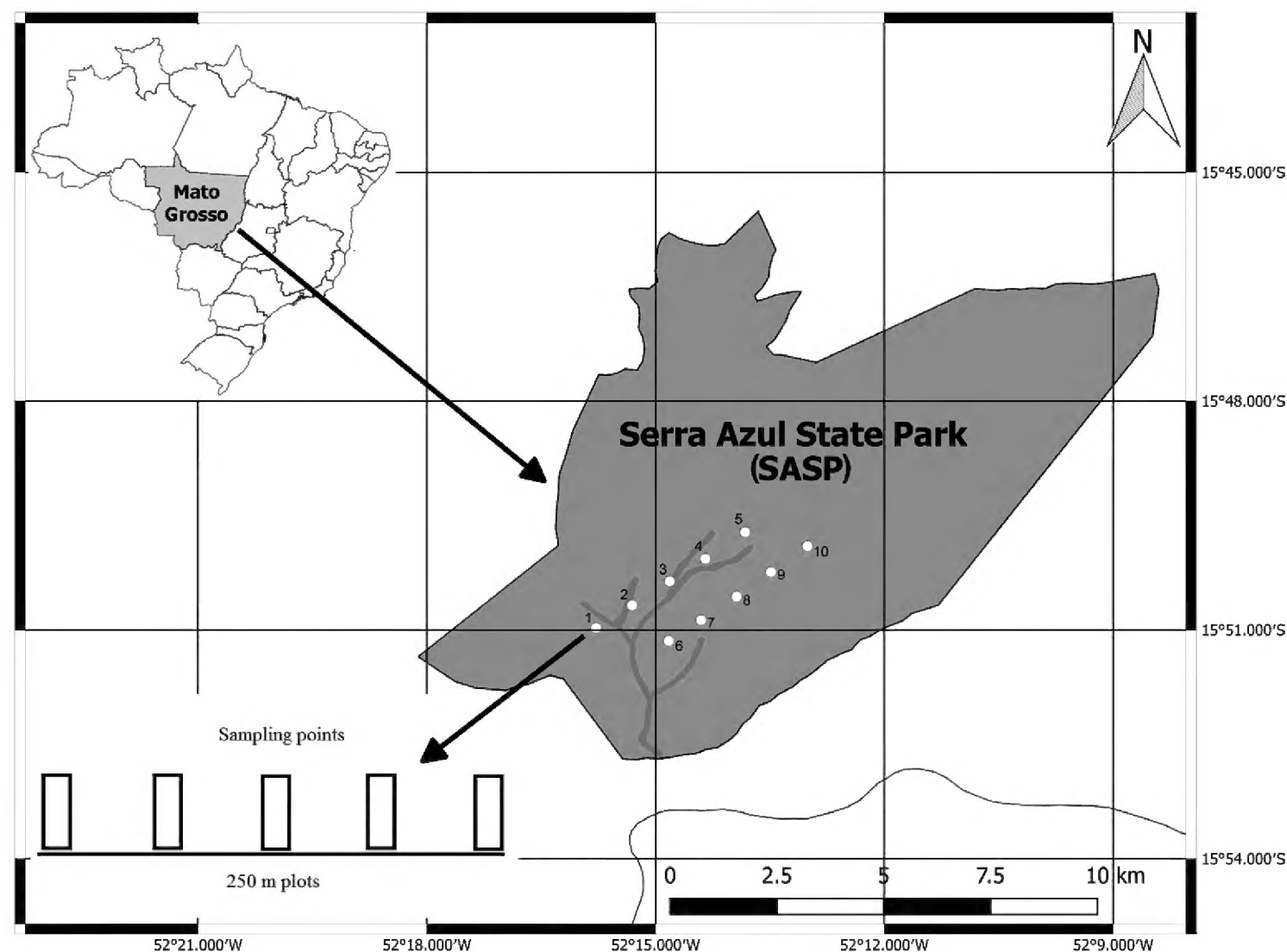
Figure 1. Map indicating the location of the study area within the Serra Azul State Park (SASP) in the state of Mato Grosso, Brazil. The detail illustrates the spatial organization of the plots following the RAPELD protocol. Plots 1, 7, 8, and 9 – Typical savanna, Plots 2, 4, 5, and 10 – Open savanna, Plot 3 – Gallery forest, Plot 6 – Deciduous forest.

the Araguaia Campus of the Federal University of Mato Grosso. Dung beetles were identified to genus using the dichotomous key of Vaz-de-Mello et al. (2011). Species were then identified by comparison with the collection of the Entomology Sector of the Zoological Collection of the Federal University of Mato Grosso (CEMT) in Cuiabá, where the material was then deposited.

Community comparisons between plant formations included only captures from pitfalls, while captures from all traps were used in community-wide summaries of guilds and total species richness. We compared species diversity among the plant formations using sample-size-based rarefaction and extrapolation curves (Magurran and McGill 2011), using the iNEXT function in the package iNEXT (Hsieh et al. 2020) only for Hill numbers of $q = 0$ (species richness) with the maximum reference sample size (Chao et al. 2014). We compared the proportion of individuals and species in each of the guilds among plant formations using the Chi-square test. In addition, we plotted the standardized abundance rank by $\log_{10(n+1)}$ in the four habitats, which allowed us to compare species richness and abundances among the habitat types.

As the distance between samples within each plot is short and dung beetles are volant and search for resources, spatially close samples may show greater similarity in species composition than distant samples, causing spatial autocorrelation. To test for spatial autocorrelation of the dung beetle community we used Mantel correlogram (Legendre and Legendre 2012). The data was first detrended so that second-order stationarity must be met and the number of the distance class was calculated using Sturge's rule (Borcard et al. 2018). The standardized Mantel statistic has the same formula as the Pearson correlation coefficient, but it is computed between the values in distance or similarity matrices X and Y (Borcard and Legendre 2012). The condition of normality was relaxed because significance was tested using permutation. The statistics were tested for significance using 999 permutations and plotted against distance classes to form the Mantel correlogram. A positive (or negative) correlation (rM) indicates that for the given distance class, the multivariate similarity among sites is greater than (or less than) that expected by chance (Borcard and Legendre 2012).

In the case of important spatial autocorrelation, we used Distance-Based Moran's Eigenvector Maps (dbMEM) as a means of quantifying the spatial effect in spatial distribution of the dung beetles community. We used Euclidean distances and the function "dbmem" in the adespatial package (Dray et al. 2020). This generated nine dbMEM that may represent the effect of dispersion as well as unmeasured variables that are also spatially structured (Peres-Neto and Legendre 2010, Fernandes et al. 2014). The dbMEMs used in the non-parametric multivariate analysis of

variance (PERMANOVA) were selected using the forward selection routine (forward.sel) in the adespatial package (Dray et al. 2020).

To compare the community structure among plant formations [F] and control for the effects of spatial structure [S], and their interactions [F|S] (if any), we used PERMANOVA (Anderson 2001). A dissimilarity matrix was calculated using Bray-Curtis distances with the Hellinger transformation (Legendre and Gallagher 2001, Legendre and Legendre 2012). We compared dung beetle species among plant formations using the pairwise.perm.manova function in the package RVAideMemoire (Hervé 2020). Additionally, we used PERMDISP (analysis of multivariate homogeneity of group dispersions) to identify location or dispersion effects (Anderson and Walsh 2013) using the function "betadisper" in the vegan package (Oksanen et al. 2020). We graphically illustrate the distributions of dung beetle assemblages in the different plant formations using Principal Coordinates Analysis (PCoA) (Legendre and Legendre 2012). As with PERMANOVA, species compositions were used to estimate dissimilarity matrices between formations using Bray-Curtis distances after Hellinger transformation. In addition, dbMEM were also represented by vectors in the PCoA that illustrate the relationship between spatial attributes and communities of dung beetles in these plant formations. Vectors were derived with the function "envfit" of the vegan package (Oksanen et al. 2020). All analyses were carried out using R (R Core Team 2020).

RESULTS

A total of 5400 dung beetles were collected, comprising 57 species, 22 genera and the following tribes: Coprini, Deltochilini (14 species each), Ateuchini (13 spp.), Phanaeini (12 spp.), Eurysternini, and Onthophagini (2 spp. each) (Table 1). Pitfalls captured 5023 individuals (93.01% of the total) and 54 species (94.74% of the total). Flight interception traps captured 377 individuals (6.98%) and 32 species (56.14% of the total species richness) and three exclusive species (*Anomiopus* sp. 2, *Anomiopus* sp. 4, *Coprophanaeus cyanescens* d'Olsoufieff, 1924) (Table 1).

The greatest number of species (47 spp., 82.45% of the total) and greatest abundance (1962 individuals, 36.33% of the total) were from typical savanna. Open savanna followed with 39 species (68.42%) and 1804 individuals (33.40%). Deciduous forest had 21 species (36.84%) and 256 individuals (4.74% of the total), while gallery forest had 18 species (31.57%) and 1378 individuals (25.51%), of which 1032 (74.89%) were of a single species, *Eurysternus caribaeus* (Herbst, 1789) (Table 1). Sample-size-based rarefaction and extrapolation curves showed that overall species richness (q = 0) was similar between the two savanna formations and the grand total from all plant formations (Fig. 2). The two forest formations were the least diverse, but the overlapping confidence intervals of the deciduous forest indicates no difference with the open savanna (Fig. 2). The richness estimated for the typical savanna was 59 dung beetle species, followed by open savanna with 49 species, deciduous forest with 27, and gallery forest with 11 (Fig. 2).
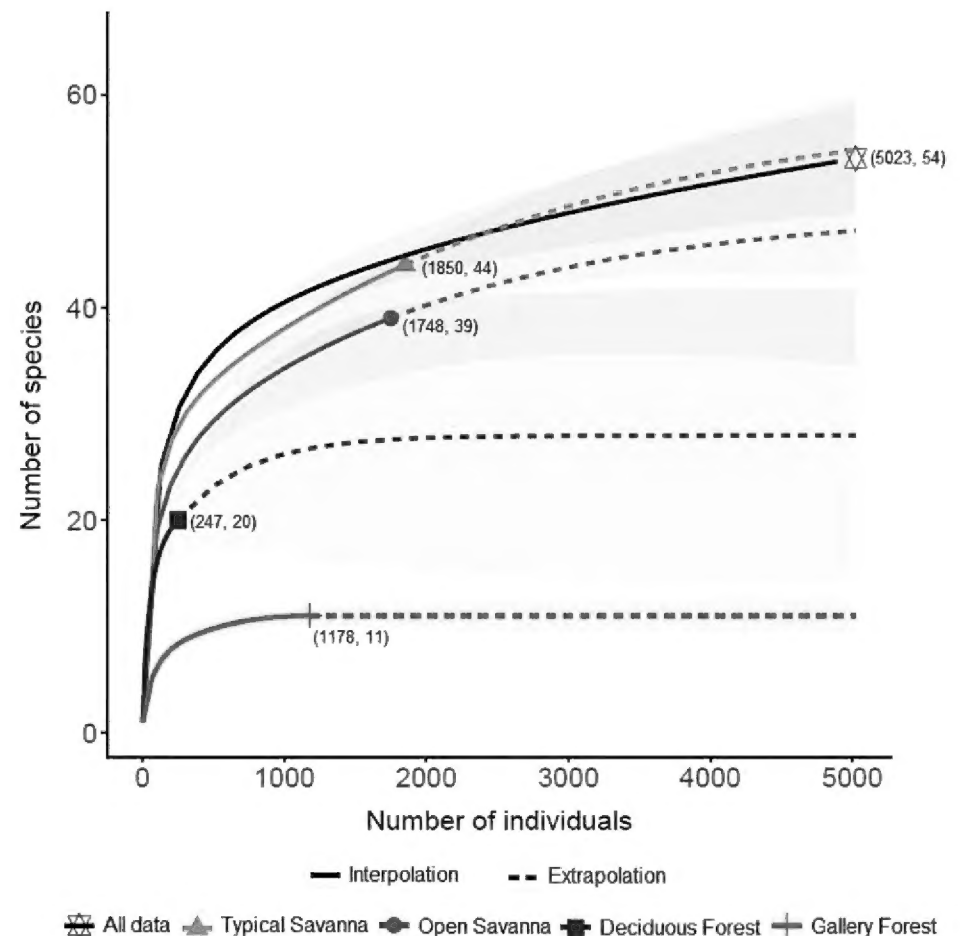

Figure 2. Sample-size-based rarefaction and extrapolation sampling curves (q = 0) of dung beetles collected with pitfall traps in the Serra Azul State Park (SASP), state of Mato Grosso, Brazil. The numbers in parentheses are the sample size and the observed Hill numbers for each reference sample. Shaded areas represent 95% confidence intervals.

Of the 47 species in the typical savanna, 12 were exclusive (25.53%), while in the open savanna, only three were exclusive (7.69%, *Canthidium* sp. 27; *Deltorhinum bilobatum* Génier, 2010, *Trichillum externepunctatum* Preudhomme de Borre, 1886). Five species were exclusive in the two forests (*Anomiopus* sp. 4, *Canthidium* sp. 16, *Canthon chalybaeus* Blanchard, 1845, *C. cyanescens*, *Oxysternon conspicillatum oberthueri* Arnaud, 2002) (Table 1).

Tunneling dung beetles were the most species-rich (29 species, 50.87% of the total), followed by rollers (12 spp., 21.05%), and dwellers (7 spp., 12.28%). Tunneling beetles were also the most abundant, with 2365 individuals (43.79% of the total), followed by dwellers (1842, 34.11%), and rollers (822, 15.22%). Nine species (371 individuals) could not be placed in any particular guild (Table 1). The proportion of species per guild was independent of plant formation (tunnelers – $\chi^2 = 0.84$, p = 0.83; rollers – $\chi^2 = 0.81$, p = 0.84; dwellers – $\chi^2 = 0.79$, p = 0.85), with the tunnelers having the most species in all formations, followed by rollers and dwellers (Fig. 3). However, relative abundance varied by habitat (tunnelers – $\chi^2 = 32.69$, p < 0.001; rollers – $\chi^2 = 40.46$, p < 0.001; dwellers – $\chi^2 = 62.171$, p < 0.001), with the tunnelers having the most individuals in almost all formations, except in the gallery forest, where dwellers were the most abundant, and both forests had fewer rollers (Fig. 3).

Table 1. Dung beetle species collected in the four plant formations in Serra Azul State Park (SASP) in the state of Mato Grosso, Brazil. (TS) typical savanna, (OS) open savanna, (DF) deciduous forest, (GF) gallery forest. Guilds: (T) Tunnelers, (R) Rollers, (D) Dwellers, (U) Unknown. (FIT) Flight interception traps. (*) Number according to reference collection of the Entomology Sector of the Zoological Collection of the Federal University of Mato Grosso (CEMT) in Cuiabá.

Species	Savanna		Forest		Total	Guild	Method	
	TS	OS	DF	GF			FIT	Pitfall
Ateuchini	201	228	15	35	479	–	–	–
Agamopus unguicularis (Harold, 1883)	1				1	R		1
Ateuchus aff. histrio	12	1			13	T		13
Ateuchus aff. pygidialis	37	4	5		46	T	1	45
Besourenga amarillai (Aguilar-Julio, 2001)	1	3			4	D		4
Besourenga sp. 1*	33				33	D		33
Deltorhinum bilobatum Génier, 2010		1			1	U		1
Genieridium bidens (Balthasar, 1942)	4	11			15	D		15
Genieridium cryptops (Arrow, 1913)	4				4	D		4
Trichillum externepunctatum Preudhomme de Borre, 1886		1			1	D		1
Uroxys sp. 1*	78	104	1	17	200	U	36	164
Uroxys sp. 3*	18	95	3		116	U		116
Uroxys sp. 10*		7	6	18	31	U	2	29
Uroxys sp. 13*	13	1			14	U		14
Coprini	652	385	70	227	1334	–	–	–
Canthidium aff. barbacenicum	191	89	4		284	T	37	247
Canthidium aff. viride	34				34	T		34
Canthidium decoratum (Perty, 1830)	116	7			123	T	12	111
Canthidium sp. 16*			7	3	10	T	4	6
Canthidium sp. 23*	19	27		2	48	T	1	47
Canthidium sp. 27*		2			2	T		2
Dichotomius aff. carbonarius	14	13	47	206	280	T	81	199
Dichotomius aff. cuprinus	1	2			3	T		3
Dichotomius aff. depressicollis	2	1	3	16	22	T	1	21
Dichotomius bos (Blanchard, 1846)	14	62			76	T		76
Dichotomius lycas (Felsche, 1901)	118	57	5		180	T	6	174
Dichotomius nisus (Olivier, 1789)	1				1	T		1
Ontherus appendiculatus (Mannerheim, 1829)	108	116	4		228	T		228
Ontherus dentatus Luederwaldt, 1930	34	9			43	T		43
Deltochilini	287	491	7	42	827	–	–	–
Anomiopus sp. 2*	2				2	U	2	
Anomiopus sp. 3*		1		1	2	U	1	1
Anomiopus sp. 4*				2	2	U	2	
Canthon aff. simulans	28	364			392	R	18	374
Canthon chalybaeus Blanchard, 1845			1	2	3	R	2	1
Canthon fortemarginatus Balthasar, 1939	171	54			225	R	3	222
Canthon histrio (Lepeletier de Saint-Fageau & Audinet-Serville 1828)	1	18	2	11	32	R	5	27
Canthon lituratus (Germar, 1813)	30	1			31	R		31
Canthon sp. 3*	1				1	R		1
Canthonella sp. 3*	1	14			15	R		15
Deltochilum enceladus Kolbe, 1893	2	2	1	22	27	R	9	18
Deltochilum pseudoicarus (Balthasar, 1939)	2	2			4	R	1	3
Deltochilum sp. 6*	39	35	3	4	81	R	38	43
Malagoniella aeneicollis (Waterhouse, 1890)	10				10	R		10
Eurysternini	331	357	60	1037	1785	–	–	–
Eurysternus caribaeus (Herbst, 1789)	8	8	17	1032	1065	D	61	1004
Eurysternus nigrovirens Génier, 2009	323	349	43	5	720	D	9	711
Onthophagini	125	212	88	19	444	–	–	–
Onthophagus aff. hirculus	50	38	87	19	194	T		194
Onthophagus buculus Mannerheim, 1829	75	174	1		250	T		250

Continues

| Species	Savanna		Forest		Total	Guild	Method	
	TS	OS	DF	GF			FIT	Pitfall
Phanaeini	366	131	16	18	531	–	–	–
Coprophanaeus acrisius (MacLeay, 1819)	2	4			6	T	5	1
Coprophanaeus cyanescens d'Olsoufieff, 1924				4	4	T	4	
Coprophanaeus spitzi (Pessôa, 1934)	6				6	T	5	1
Dendropaemon denticollis Felsche, 1909	2	1			3	U	2	1
Diabroctis mimas (Linnaeus, 1758)	16	13	2		31	T	1	30
Diabroctis mirabilis (Harold, 1877)	2				2	T		2
Oxysternon conspicillatum oberthueri Arnaud, 2002			9	13	22	T	11	11
Oxysternon palemo Castelnau, 1840	284	106			390	T	10	380
Oxysternon silenus Castelnau, 1840	1		5	1	7	T	1	6
Phanaeus kirbyi Vigors, 1825	3				3	T	1	2
Phanaeus melibaeus Blanchard, 1846	1				1	T		1
Phanaeus palaeno (Blanchard, 1846)	49	7			56	T	5	51
Richness	47	39	21	18	57	–	32	54
Richness %	82.45	68.42	36.84	31.57	–	–	56.14	94.73
Abundance	1962	1804	256	1378	5400	–	377	5023
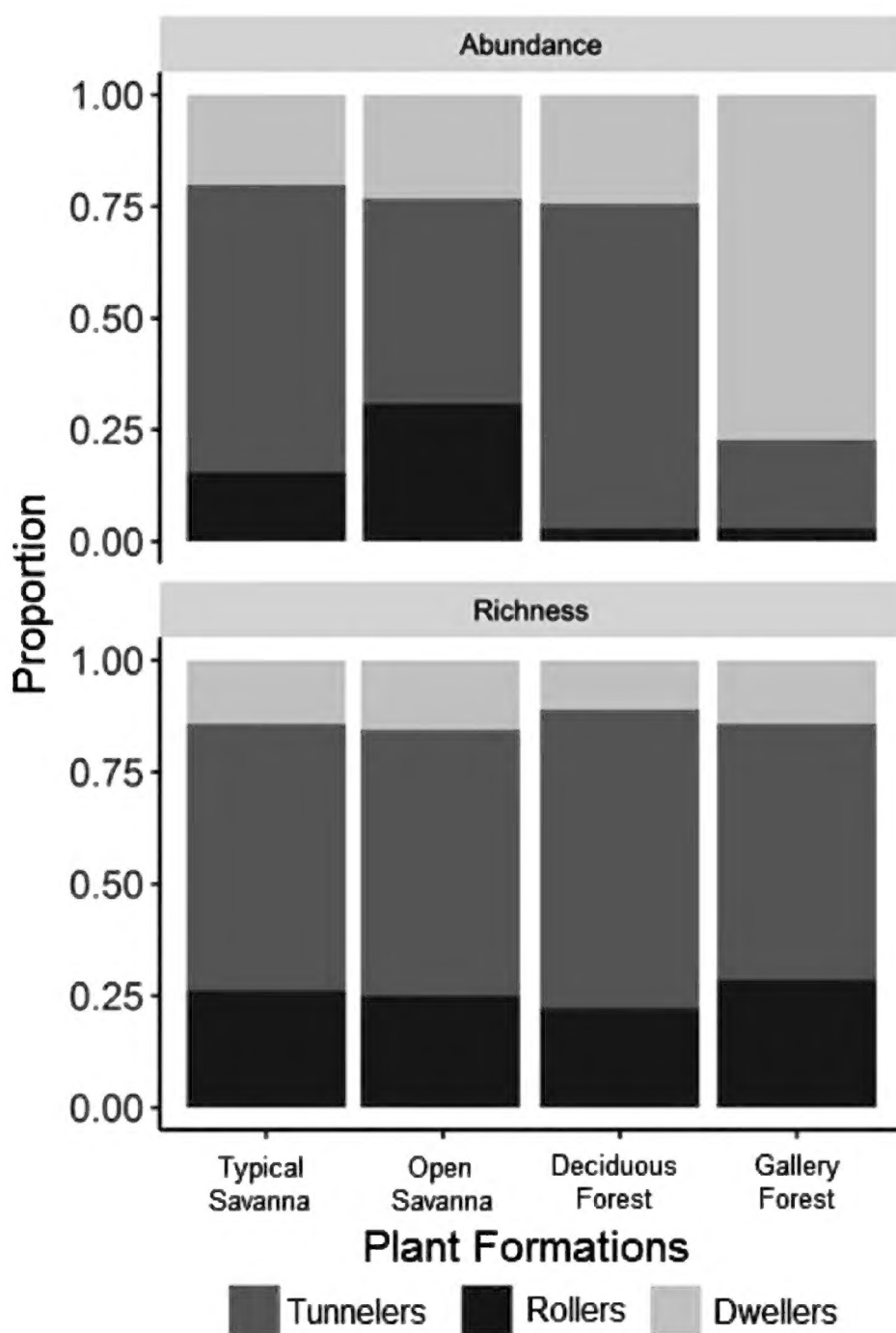
Figure 3. Proportions of the three guilds of dung beetle by abundance and richness compared among the four plant formations in the Serra Azul State Park (SASP), summing both trap types (pitfall, FIT).

While in the gallery forest, where one dweller species (*E. caribeus*) comprised 74.89% of the individuals collected, the two savanna formations were more similar and had no strongly numerically dominant species (Fig. 4). Thus, in both savanna formations, *Eurysternus nigrovirens* Génier, 2009 was the most common species, and *Oxysternon palemo* Castelnau,
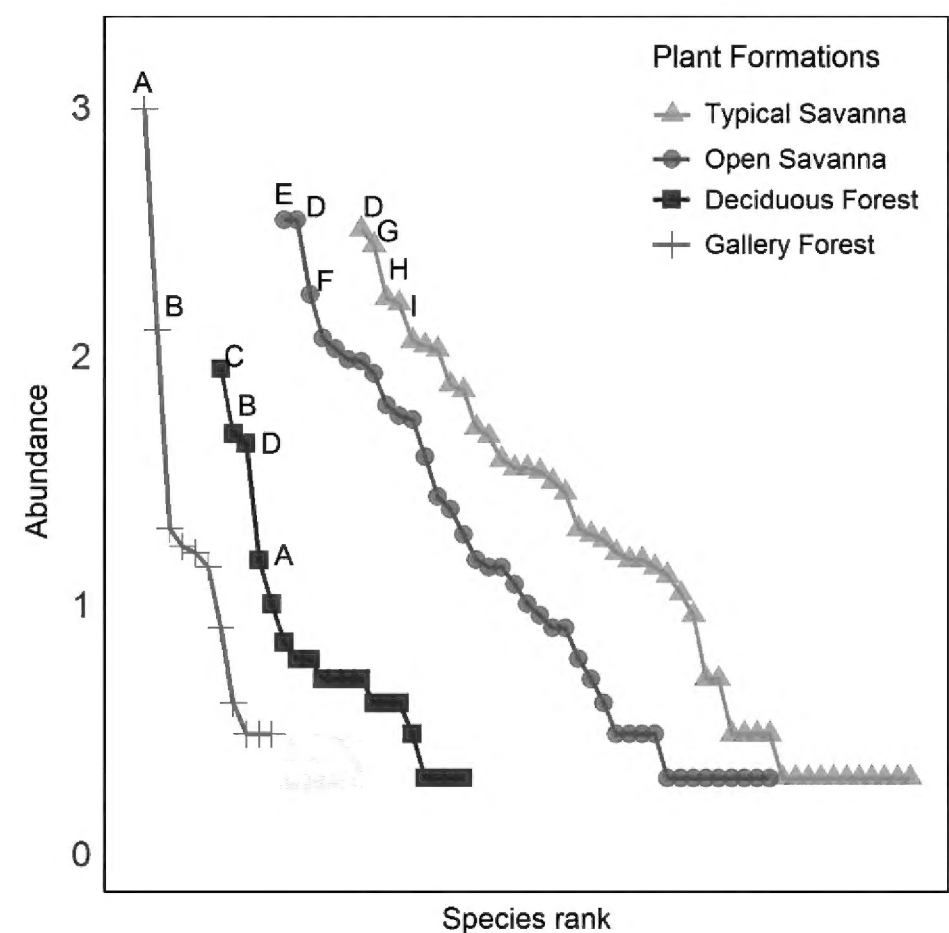

Figure 4. Rank abundances of dung beetles compared among the four plant formations in the Serra Azul State Park (SASP), state of Mato Grosso, Brazil. The letters indicate the more abundant species: (A) *Eurysternus caribaeus*, (B) *Dichotomius* aff. *carbonarius*, (C) *Onthophagus* aff. *hirculus*, (D) *Eurysternus nigrovirens*, (E) *Canthon* aff. *simulans*, (F) *Onthophagus buculus*, (G) *Oxysternon palemo*, (H) *Canthon fortemarginatus*, (I) *Canthidium* aff. *barbacenicum*.

1840 and *Canthon* aff. *simulans* were equally abundant in both savanna formations. In the forested sites, aside from the previously mentioned *E. caribaeus*, *Dichotomius* aff. *carbonarius* was relatively abundant in both. However, in the deciduous forest, *Onthophagus* aff. *hirculus* was somewhat more abundant than *D.* aff. *carbonarius*, which was followed by *E. nigrovirens*; the latter was common in the savannas (Fig. 4).

The Mantel Correlogram indicated that spatial autocorrelation existed. At the first distance class (i.e., 29.06 to 471.63 m), the correlation was strongest and positive (r = 0.37, p = 0.001), and weaker and negative (r = -0.20, p = 0.001) at the second distance class (i.e., 471.63 to 914.63 m). Thus, spatial autocorrelation was found at less than 914 m (Fig. 5). All subsequent correlations were |r| < 0.19, indicating that any additional spatial autocorrelation was relatively unimportant (see supplementary material for more details, Table S1).
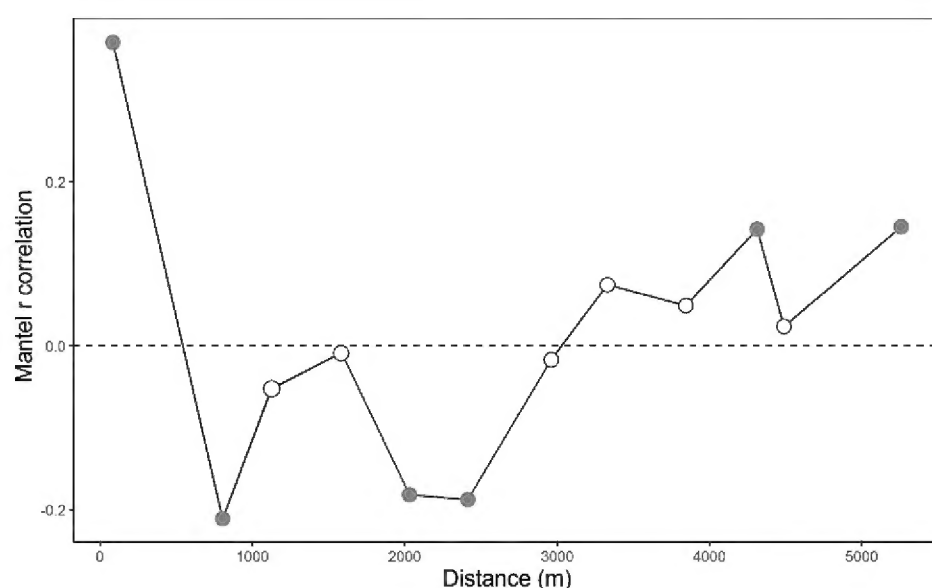

Figure 5. Mantel correlogram between dung beetle community and pairwise distance of plots in the four plant formations of the Serra Azul State Park (SASP), state of Mato Grosso, Brazil. Positive significant values indicate a positive autocorrelation, while significant negative values have the opposite interpretation. Significant values are represented by red circle.

The two first PCoA axes explain ~51% of the variation in the dung beetle community and separate the two savannas from the two forests (Fig. 6). This ordination was correlated with several spatial attributes (dbMEM1: r^2 = 0.31, p < 0.001; dbMEM2: r^2 = 0.51, p < 0.001; dbMEM4: r^2 = 0.13, p = 0.03; dbMEM6: r^2 = 0.19, p < 0.01) (Fig. 6). The results of PERMANOVA confirmed the visually observed differences in species composition between the four studied vegetation types (PERMANOVA, r^2 = 0.52, F = 34.4, p = 0.001). A posteriori tests found that all plant formations were different (p < 0.01 for all comparisons). In addition to plant formation [F], space [S] explained 23% of the variation in dung beetle community structure (PERMANOVA: r^2 = 0.23, F = 6.7, p = 0.001), while 12% were explained by the interaction between plant formations and space [F|S] (PERMANOVA: r^2 = 0.12, F = 1.5, p = 0.014). The dispersion heterogeneity

(calculated using PERMDISP) demonstrated that the differences among the four plant formations ($F_{3,46}$ = 8.86; p < 0.001) were mostly due to gallery forest with the lowest average distance to the median (0.11) when compared to open savanna (0.33), typical savanna (0.29), and deciduous forest (0.30).
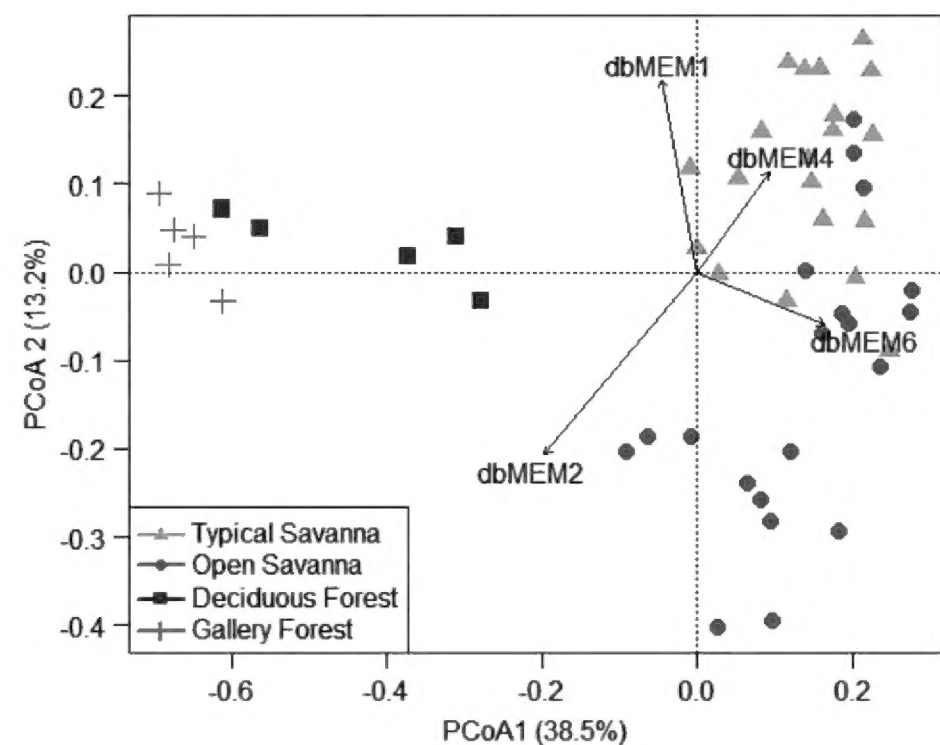

Figure 6. Ordination (PCoA) of the beetle assemblages in each plant formation in Serra Azul State Park (SASP), state of Mato Grosso, Brazil, with the vectors of spatial attributes (dbMEM).

DISCUSSION

Dung beetle communities are more species-rich and species are more abundant in the savanna as compared to forest formations in the SASP. In addition, species composition and guild structure varied between the two formations. Dung beetles are diverse in the Brazilian Cerrado (mostly savanna, but within which are patches of gallery and dry-deciduous forests, much like those we examined here), where savanna formations tend to be more diverse and species-rich than forests (Milhomem et al. 2003, Endres et al. 2007, Silva et al. 2010). The tribes Coprini, Deltochilini, Ateuchini, and Phanaeini were the most speciose (Costa et al. 2009, Daniel et al. 2014, Silva et al. 2014), and they also tend to be more common and diverse in the savanna formations. We collected a total of 57 species in a region where more than 50 are often collected (Milhomem et al. 2003, Almeida and Louzada 2009, Daniel et al. 2014), but our interpolation and extrapolation curves suggest that more than 70 species may eventually be found in the Cerrado as a whole (Fig. 2).

The SASP is in a region where dung beetles are common and diverse (southwestern Brazilian Cerrado). For example, *Besourenga amarillai* (Aguilar-Julio, 2001), *Canthidium barbacenicum* Preudhomme de Borre, 1886, *Canthidium decoratum* (Perty, 1830), *C.* aff. *simulans*, *Canthon fortemarginatus* Balthasar, 1939, *Dichotomius lycas* (Felsche, 1901), *E. nigrovirens*, *Genieridium cryptops* (Arrow, 1913), *Onthophagus buculus* Mannerheim, 1829, *O. palemo*, and

Phanaeus kirbyi Vigors, 1825 are often found in open (natural or anthropic) landscapes in central South America (in the Cerrado and Chaco formations; Edmonds 1994, Aguilar-Julio 2001, Edmonds and Zidek 2004, Vaz-de-Mello 2008, Almeida and Louzada 2009, Génier 2009, Daniel et al. 2014, Silva et al. 2014, Tissiani et al. 2017, Vaz-de-Mello et al. 2017). On the other hand, many of the species found in the forests tend to have Amazonian and Chacoan influences, along with some influence from the Atlantic Forest, e.g., *C. cyanescens*, *Deltochilum enceladus* Kolbe, 1893, *Dichotomius carbonarius* (Mannerheim, 1829), *Oxysternon conspicillatum* (Weber, 1801), and *Oxysternon silenus* Castelnau, 1840 (Edmonds and Zidek 2004, 2010, Génier 2012, Vaz-de-Mello et al. 2017).

Most species captured in all habitat types were tunnelers, followed by rollers and dwellers, a result that appears to be the general pattern for dung beetles in the Neotropical region (Halffter et al. 1992, Louzada and Lopes 1997, da Silva and Di Mare 2012, Campos and Hernández 2013, Silva et al. 2015). In addition to being the most diverse group, tunnelers are also the most abundant dung beetles in all habitat types. Although in the same guild, tunneler habits are not identical; different species have different patterns of tunneling, beneath or alongside the feces, and this variation perhaps allows more species to use the same resource in different ways, thereby avoiding competition, a point that may explain the greater abundance of this group (Daniel et al. 2014, Silva et al. 2015).

Both rollers and dwellers are also more abundant and species-rich in the savanna formations, with the exception of the dweller *E. caribaeus*, which was super-abundant in the gallery forest. This is surprising because the more humid environment of the forest is expected to generate microclimates that favor these guilds because feces should dry more slowly (Hanski and Cambefort 1991). It is noteworthy that the interaction between tree density, canopy height, and microclimate is complex. Thus, because the range of tree density in the savanna formations may be greater than in the two forest types (while canopy height is always greater in the forests), tree density in savannas may sometimes generate the microclimate that favors rollers and dwellers. Testing the fine details that determine habitat quality for dung beetles was outside the scope of this study, but future ecological studies should measure microhabitats at the point of capture to better understand these dynamics in the SASP.

No single species was dominant in the savanna formations where two or more species tended to be similarly abundant, in contrast to the forests, especially gallery forest. Dominance has been found in some dung beetle assemblages in both savannas and forests (Almeida and Louzada 2009). Varying patterns of dominance may be explained in part by resource abundance (or scarcity), where species may be co-dominant (Kadiri et al. 1997), or due to habitat modification (Halffter et al. 1992, Halffter and Arellano 2002, Nichols et al. 2007), or perhaps even time of year when collections took place. Future study should examine these possibilities, especially with respect to the surprisingly abundant *E. caribaeus* in the gallery forest.

Some spatially structured processes may also influence local species compositions in dung beetle communities (Louzada et al. 2010). Thus, for understanding dung beetle assemblages in the SASP, dispersal, habitat heterogeneity, and human-caused modifications may all be important spatial processes. In the Brazilian Cerrado, habitat heterogeneity is due to the variety of plant formations (Silva et al. 2010). These authors compared dung beetle communities in forest and savanna in Chapada dos Parecis, Mato Grosso, showing that less heterogeneity in savanna habitats ("campos sujos") caused greater species richness than in gallery forest (with greater heterogeneity), a point that could explain our results. Alternatively, the greater heterogeneity of habitats (related to a greater number of plant species and greater plant stratification) may promote greater richness and abundance of dung beetles (Almeida and Louzada 2009). In the SASP, studies demonstrated that many species that are often very abundant are found in typical savanna habitats, and that plant cover increases with rainfall (Pirani et al. 2009, Santos et al. 2017), when we carried out this study. Thus, it is possible that the variety of species and their abundance in the typical savanna is due to the variety of habitats available as a consequence of structural complexity.

Although the SASP is a protected area for conservation, anthropic pressures, such as forest fires, can influence habitat structure and availability, thereby influencing the dung beetle community. For example, forest fires occurred in 2002, 2005, and 2007, when the entire Park burned (Ribeiro et al. 2012). In the savanna, the consequences of forest fires could be less severe to plant communities than those found in forests (Peixoto et al. 2012, Ribeiro et al. 2012). Because fires influence indirectly dung beetle communities through habitat modification (Louzada et al. 1996, 2010, de Andrade et al. 2014), we predict that fires will have a smaller impact on dung beetle communities in savannas than in forests because of the smaller effect fires have on savannas.

Considering the history of SASP occupation and its surroundings, deforestation is cited as one of the most important anthropic pressures on the Park (FEMA 2000, Santos et al. 2006), causing fragmentation and loss of habitat. The influences on dung beetle communities of the size of the habitat fragment, its isolation, and the surrounding matrix have been mentioned in several studies (Estrada and Coates-Estrada 2002, Milhomem et al. 2003, Nichols et al. 2007, Filgueiras et al. 2011). As SASP is within a predominant savannah matrix (FEMA 2000, Peixoto et al. 2012), we infer that forests were more strongly influenced by isolation and habitat loss, thus reducing the richness and abundance of beetle species in these formations, especially the gallery forests that may present communities most affected by these factors (Milhomem et al. 2003, Silva et al. 2010).

We consider that this regional landscape mosaic, formed by combinations of forests and savannas of the Brazilian Cerrado, has been an important determinant of the dung beetle communities found in the SASP. For these reasons, regional

diversity is very high. We believe that additional measures are necessary for protecting the SASP. These measures should take into account the complex matrix of habitat types and species that occur in each of these habitats (Almeida and Louzada 2009). Additionally, we recommend that conservation efforts should be directed towards reducing anthropic pressures within the SASP. These actions would favor stability of the distinct habitats. Such stability would in turn be beneficial for the dispersal of dung beetles among habitat types in the area.

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